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POPULATION DYNAMICS OF AN URBAN POPULATION OF THE LAND SNAIL *MARMORANA SERPENTINA* (GASTROPODA: PULMONATA)

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INTRODUCTION

Spatial distribution, population structure, and dispersal patterns are fundamental characteristics of species. When the area occupied by a population far exceeds the dispersal ability of individuals, random mating cannot be assumed over the entire population. Wright (1946) introduced the concept of "neighbourhood" for cases in which individuals have only a limited number of potential partners, their neighbours. Neighbourhoods are restricted areas where random mating is likely. Study of the population structure and understanding of speciation processes depend on accurate data on movement patterns, dispersal capacity, and density (Parmakelis & Mylonas, 2004).

Land snails are particularly subject to population subdivision and geographic structuring due to their low dispersal capacity and frequent restriction to calcareous substrata. Active dispersal of terrestrial gastropods is influenced by such factors as population density, habitat complexity, climatic conditions, body size, and homing tendency (Cowie, 1980; Baker, 1988; A. Baur & B. Baur, 1990; Aubry, 2006).

This paper reports a study of population structure and monthly and daily activity of a non-native population of the land-snail species *Marmorana serpentina* (Férussac, 1821) living in the walls of the fortress of Siena, Italy. This species occurs in Sardinia and Corsica, but a few introduced populations are also present in Tuscany originating from passive transport by humans. *Marmorana serpentina* is a medium-size snail (1.5–2.0 cm shell diameter). It has a life cycle of at least three years. It inhabits rocky, preferably calcareous substrata. Mating occurs in spring and autumn with a period of aestivation between. Eggs are usually deposited in rock crevices and hatch after a few weeks.

MATERIALS AND METHODS

Survey Site

The study lasted from March 2006 to November 2007 and was performed at the Fortezza Medicea in Siena, a military fortress built in the sixteenth century. The fortress walls offer advantages over natural habitats. Surveys can be more exhaustive and complete. Density estimates are more accurate because of the simplified habitat surface and the high probability that a marked specimen not recaptured left the surveyed plots or died. Survey can be frequent, which is particularly important for monitoring daily activity. After a preliminary survey, the side of the fortress with the highest population density was chosen. It faces ESE and is 70 m long and 6 m high (Fig. 1).

The fortress walls were built with clay bricks cemented with lime mortar. Brick surfaces are separated by columns of sandstone every ten meters. Crevices between the bricks, homogeneous in shape, size, and distribution, provide shelter for snails.

Insolation of the wall varies during the day: for the first half of the morning sunlight illuminates only the southern half of the wall, which has a patchy cover of algae, lichens, and occasional grasses. Different lichen associations are evident on the wall: on the northern half there are only crustose lichens, such as *Physcia adscendens* and *Xanthoria parietina*; on the southern half, there are crustose lichens with a particularly developed thallus, such as *Physconia grisea*. Algal cover is abundant, especially on the northern half. More than 5 m above the ground, vegetation becomes sporadic probably due to renovation.

Marmorana serpentina occupies the first 5 m from the ground. Above this height no land snails seem to be present.

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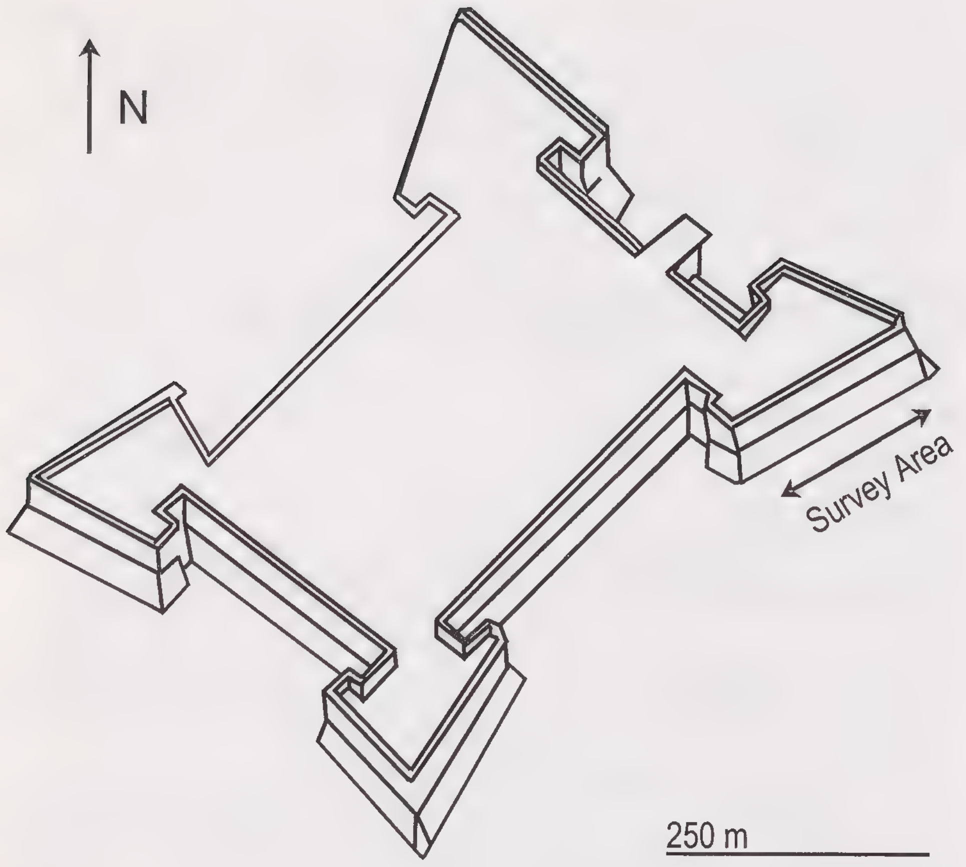

FIG. 1. The sampling site: the Renaissance Fortezza Medicea in Siena.

Data Collection

The study area was stratified into seven contiguous strips measuring 10.0 m by 2.5 m (Fig. 2). This stratification was simple because the wall is divided by columns of sandstone every 10 metres. Density was assessed by randomly placing five 1 x 1 m sampling squares per strip. Surveys were undertaken in 2006 and 2007 at intervals of at least 15 days (Table 1).

After field assessment, permanent marker was chosen as the most suitable marking method (Parmakelis & Mylonas, 2004). We searched for adult (identified by shell size and fully developed shell lip) and juvenile snails in each strip and marked them with a numerical code, when possible without detaching them from the wall or disturbing them excessively. In 2006, 106 specimens were marked on the first survey occasion (March); in 2007, 125 specimens were marked at the start (March).

Each strip was imagined as a bivariate Cartesian plan and used to record the position of marked specimens. In order to record long distance dispersal, we also searched outside the surveyed area (10 m on either side). During each survey the distance between consecutive positions of recaptured specimens was calculated – Euclidean distance:

$$d = \sqrt{(X_1 - X_2)^2 + (Y_1 - Y_2)^2}.$$

From summer 2007, daily activity and environmental variables were recorded (Table 1).

TABLE 1. Survey plan. M, marking; N, number of marked specimens; D, density; R, recapture; DA, daily activity; EV, environmental variables recorded.

N°	Date	Recorded variables
1	03-03-2006	M 1 (N = 106); D
2	19-03-2006	R; D
3	25-04-2006	R; D
4	30-05-2006	R; D
5	28-06-2006	R; D
6	01-03-2007	M 2 (N = 125); D
7	22-03-2007	R; D
8	30-04-2007	R; D
9	17-05-2007	R; D
10	31-05-2007	R; D
11	14-06-2007	R; D
12	28-06-2007	R; DA; EV; D
13	12-07-2007	R; DA; EV; D
14	03-09-2007	R; DA; EV; D
15	13-09-2007	R; DA; EV; D
16	28-09-2007	R; DA; EV; D
17	11-10-2007	R; DA; EV; D
18	26-10-2007	R; DA; EV; D
19	12-11-2007	R; DA; EV; D

During the first two daily activity surveys, the positions of recaptured specimens were taken six times (every three hours from 9 am to 12 pm), but since this timing was too intense for the low activity of the snails, from the third survey it was subsequently only recorded four times (9 am, 3 pm, 6 pm, and 12 pm). Temperature (T) and relative humidity (RH) were recorded with a Comet data logger (model S3120). Resolution and accuracy were 0.1 and ± 2.5% and 0.1 and ± 0.4°C, respectively. Three randomly located replicates of RH and T were recorded at each strip for each survey and each 1 hr (on average) time period (9.00, 15.00, 24.00). Within each survey, T and RH were recorded at the beginning and end of each time period.

Statistical Analysis

Factorial analysis of variance was used to detect differences in dependent variables (density, Euclidean distance, temperature, relative humidity) across sampling factors (strips, days, time periods). The specific factorial design depended on the variables analysed. For density and Euclidean distance, strips and days were used as crossed factors, while for days on which daily activity was studied, we analysed the dependence of Euclidean distance on strips, days, and time periods. For T and RH, a four-factor design with strips, days, time periods, and minutes (the beginning and the end of time periods) was used.

Rayleigh's test (Zar, 1984) was used to check for directional preference in individual movements: the azimuth was defined according to the ordinate axis. Many indices can be used to define population aggregation. On the basis of the survey design, we chose the mean-to-variance ratio to test the null hypothesis of regular distribution (Krebs, 1998).

The specimens recaptured at least twice in the 2007 survey were classified on the basis of the point most distant from where they were marked: (1) not vagile: within 1 m; (2) slightly vagile: beyond 1 m but within 3 m; (3) vagile: beyond 3 m. Specimens were classified as fugitive if they were no longer found and as pulsing if they were found intermittently.

Finally, in order to estimate neighbourhood size (N_S), we used the formula introduced by Wright (1946) for a continuously distributed population of randomly mating simultaneous hermaphrodites distributed in a two-dimensional habitat: $N_S = 4\pi S^2 D$, where N_S is the number of individuals in the neighbourhood area, S^2 is the variance of dispersal of adults during one generation along a single axis, and *D* is the density of breeding individuals. Following Greenwood (1976), the variance of dispersal along a single axis was calculated as half the variance of dispersal in all directions. Because previous field observations (confirmed by the results of the present study) suggested that individuals may live at least three years and probably reach maturity in the first two years, we estimated a minimum generation time of 1.5–2 years and calculated S^2 accordingly. The associated area (N_A) was calculated as a circle of radius $\sqrt{2S}$ according to Pfenninger et al. (1996).

All statistical analyses were performed with the R package (http://www.r-project.org) and STATISTICA 5 (StatSoft Inc., Tulsa, USA).

RESULTS

Population Density and Environmental Features

Population density differed significantly among strips ($F_{6, 532} = 33.2$, $P < 0.001$) and days ($F_{18, 532} = 2.1$, $P < 0.001$), but the interaction between these two factors was not signifi-

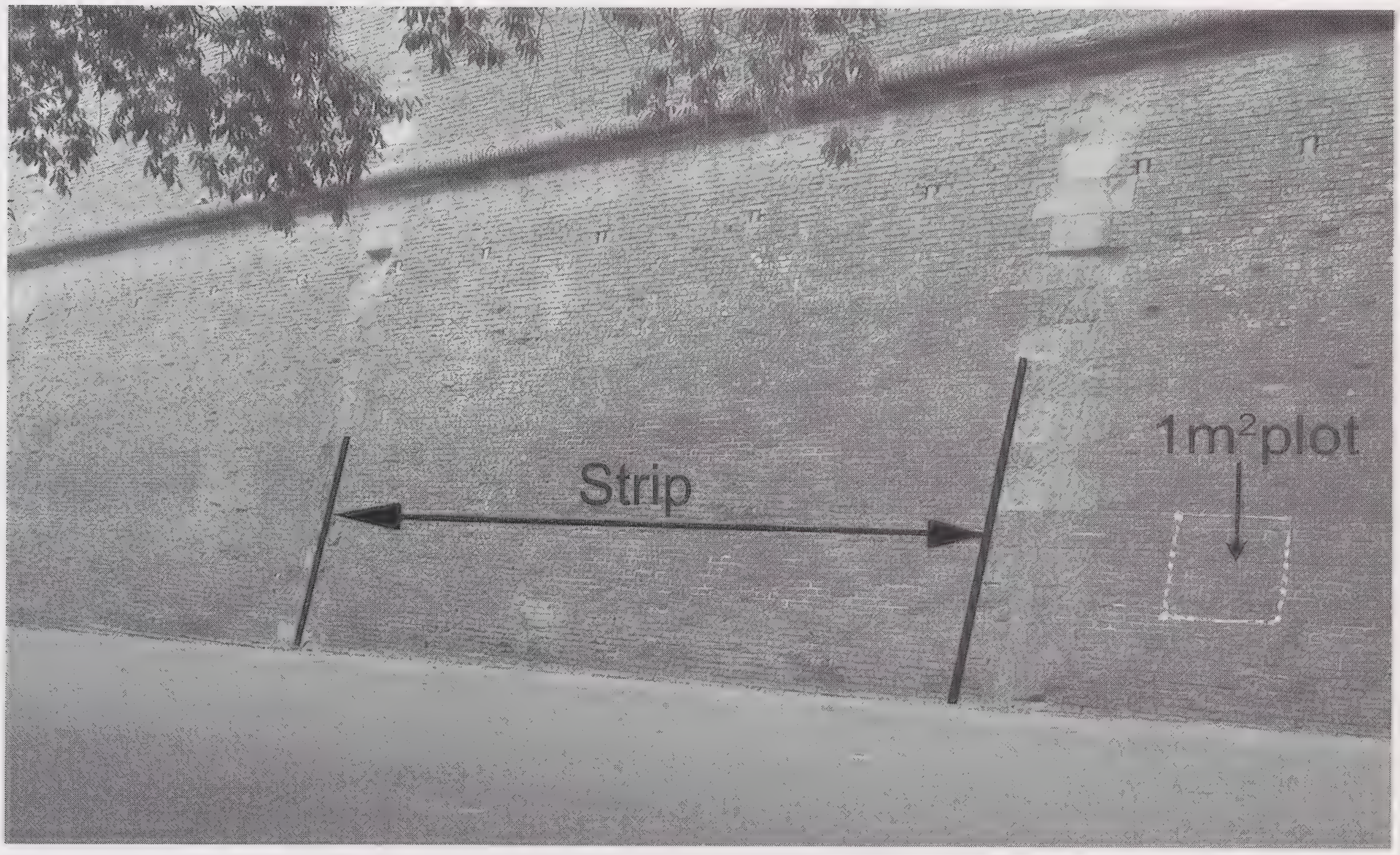

FIG. 2. Survey area stratified into seven contiguous strips and randomly placed plots of 1 m^2.

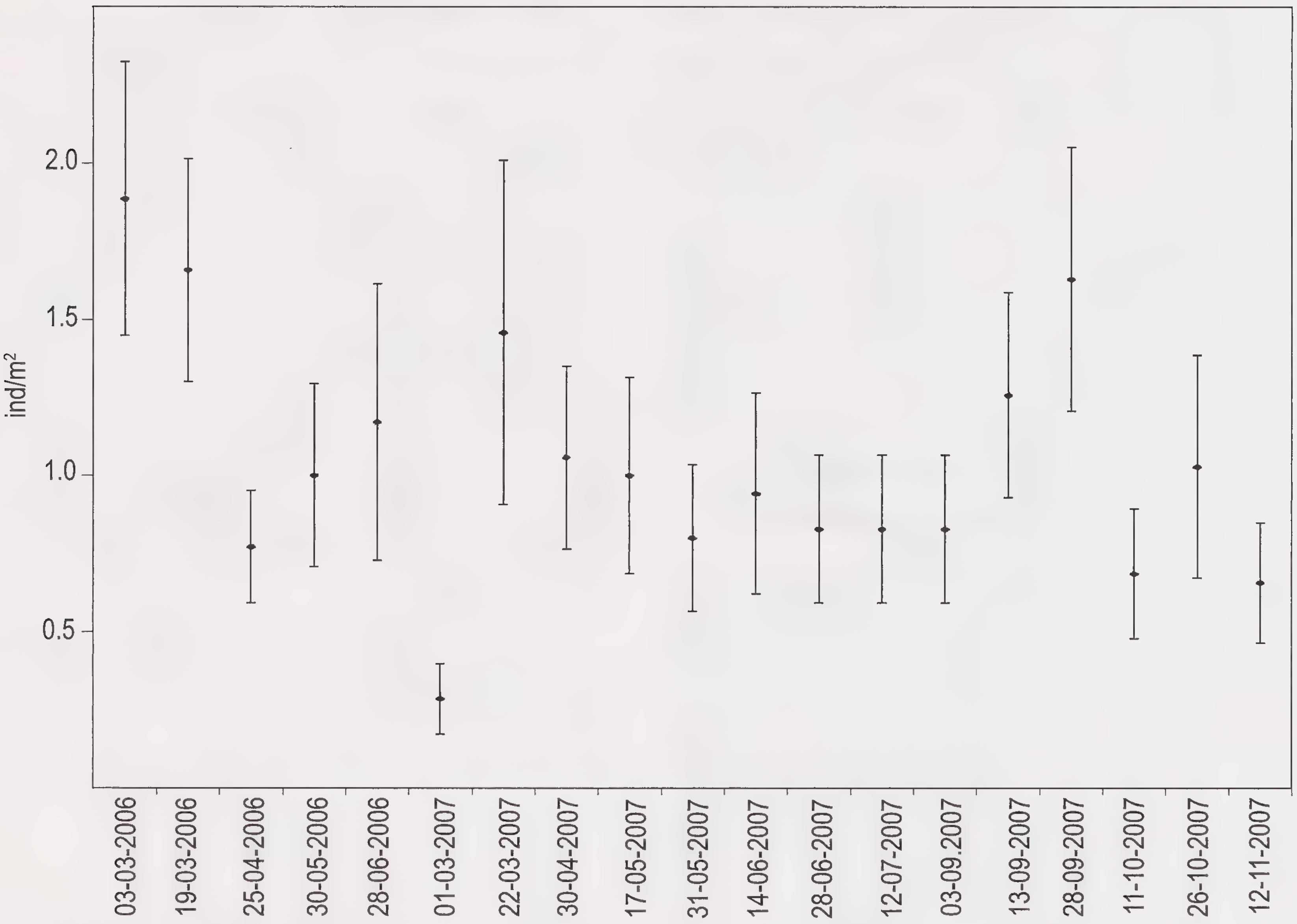

FIG. 3. Mean (± S.E.) population densities across surveys ordered chronologically from March 2006 to November 2007.

cant, indicating consistent spatial differences in time. Mean (± S.E.) density ranged from 0.2 ± 0.1 ind/m^2 (strip 6) to 2.3 ± 0.3 ind/m^2 (strip 3) and 2.4 ± 0.3 ind/m^2 (strip 2). Density decreased in the first year, culminating with the lowest observed density (0.3 ± 0.1 ind/m^2) in March 2007, after which the population recovered and oscillated around the 2006 mean of approximately 0.4 ind/m^2 (Fig. 3).

The variance-to-mean ratio test was calculated by pooling data of all days within each strip (N = 95). The aggregation index indicated that populations clustered significantly at the scale of the strips (Table 2).

The ANOVA model identified days as the main factor driving T ($F_{7, 998} = 643$, $P < 0.001$) and % RH ($F_{7, 990} = 490$, $P < 0.001$), while no significant spatial differences were detected among strips. The highest mean daily relative humidity was observed in autumn (67% RH at 18.5°C on 26 September 2007), the lowest in summer (28% RH at 25.5°C on 12 July and 13 September 2007).

Dispersal and Neighbourhood Size

Over the whole survey period, a total of 432 movements were recorded. The mean (± S.D.) percentage of recapture (Fig. 4) was 22 ± 9% in 2006 and 22 ± 7% in 2007. In the two years, six marked shells were found dead, accounting for a small percentage (< 5%) of non-recaptures.

No significant spatial variation and no differences between adults and juveniles were detected in mean Euclidean distance moved (dispersal). However, significant differences were found for adults among days ($F_{16, 318} = 5.9$, $P < 0.001$) with mean (± S.E.) distances ranging from 0.2 ± 0.1 m (28 June 2007) to 2.9 ± 0.6 m (12 November 2007) (Fig. 5). Among the eight surveys on which daily activity was

TABLE 2. Aggregation index (N = 95 for each strip).

Strip	Mean Density	Variance	χ^2 variance/mean
1	0.41	0.79	183***
2	2.39	9.73	383**
3	2.33	6.24	252**
4	0.63	0.85	127*
5	0.81	1.36	159**
6	0.17	0.22	127*
7	0.53	1.42	244**

***$P < 0.001$; **$P < 0.01$; *$P < 0.05$

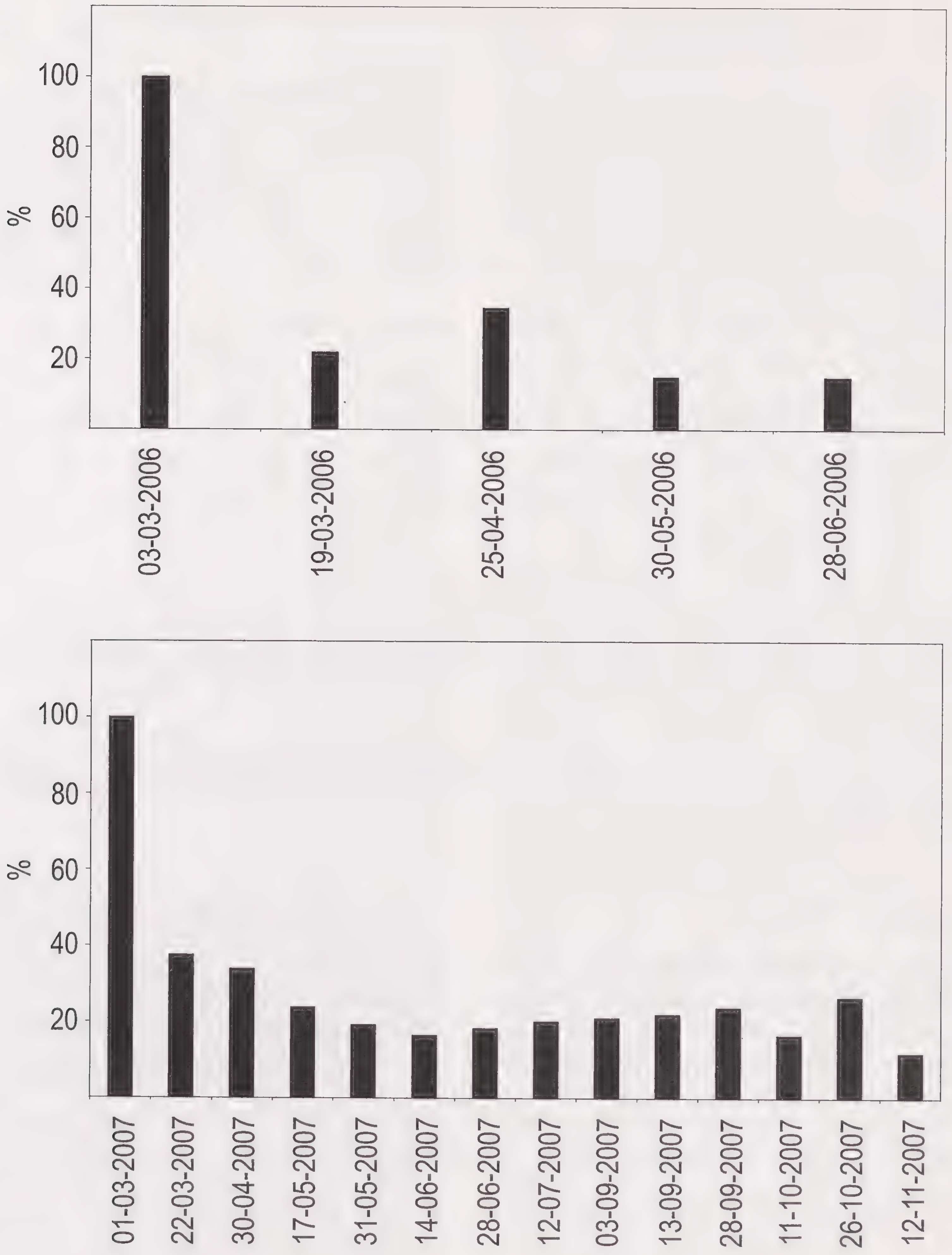

FIG. 4. Frequency distribution (percentage of total number of marked specimens) of recaptures after the initial marking date in March of each of 2006 and 2007.

studied, dispersal was only detected on rainy days. Mean (± S.E.) Euclidean distance of all measurements was 0.9 ± 0.1 m. However, observations on marked specimens showed different and apparently inconsistent movement patterns: some moved upwards or downwards and returned approximately to their original position, while others moved randomly around their starting point; some covered a total of about 3.5 m, but because they moved away and back to the starting point, the distance was only a few centimetres. Others covered a total of less than 0.5 m.

Rayleigh's test performed at several temporal scales (yearly, monthly, and daily) did not show any significant direction of dispersal, thus implying a random pattern. However, in a few cases (N = 7) specimens left the strips in which they were marked.

Chi square on the frequency distribution of the 69 specimens classified as fugitive or pulsing, to test the null hypothesis that the categories had the same frequency, demonstrated that fugitives were significantly less frequent ($\chi^2 = 32$, d.f. = 1, $P < 0.001$), whereas the frequency of the three vagility categories

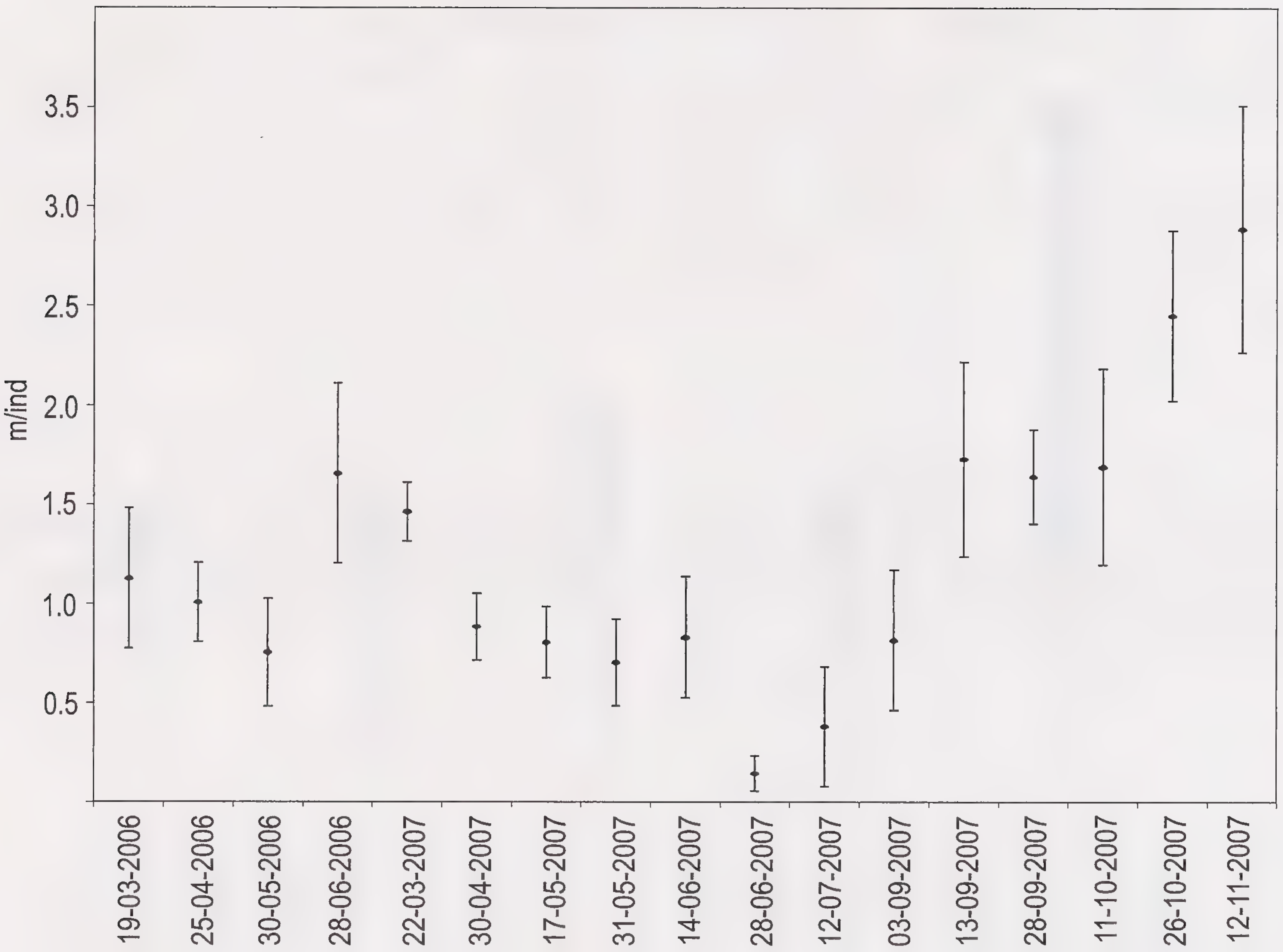

FIG. 5. Mean (± S.E.) Euclidean distance between two successive recaptures by date.

did not vary significantly ($\chi^2 = 0.72$, d.f. = 2, $P > 0.5$).

Since the strips supported different population densities and the differences remained temporally consistent, neighbourhood size and area were calculated for each strip, averaging the values obtained using the mean density observed in each strip at each date. Neighbourhood area was found to be 6.7 m^2 (radius = 1.5 m) and neighbourhood size *Ns* ($F_{6,\ 126} = 28.2$, $P < 0.001$) varied significantly from a mean (± S.E.) of 34 ± 4 in strip 2 to 2 ± 1 in strip 6 (Fig. 6).

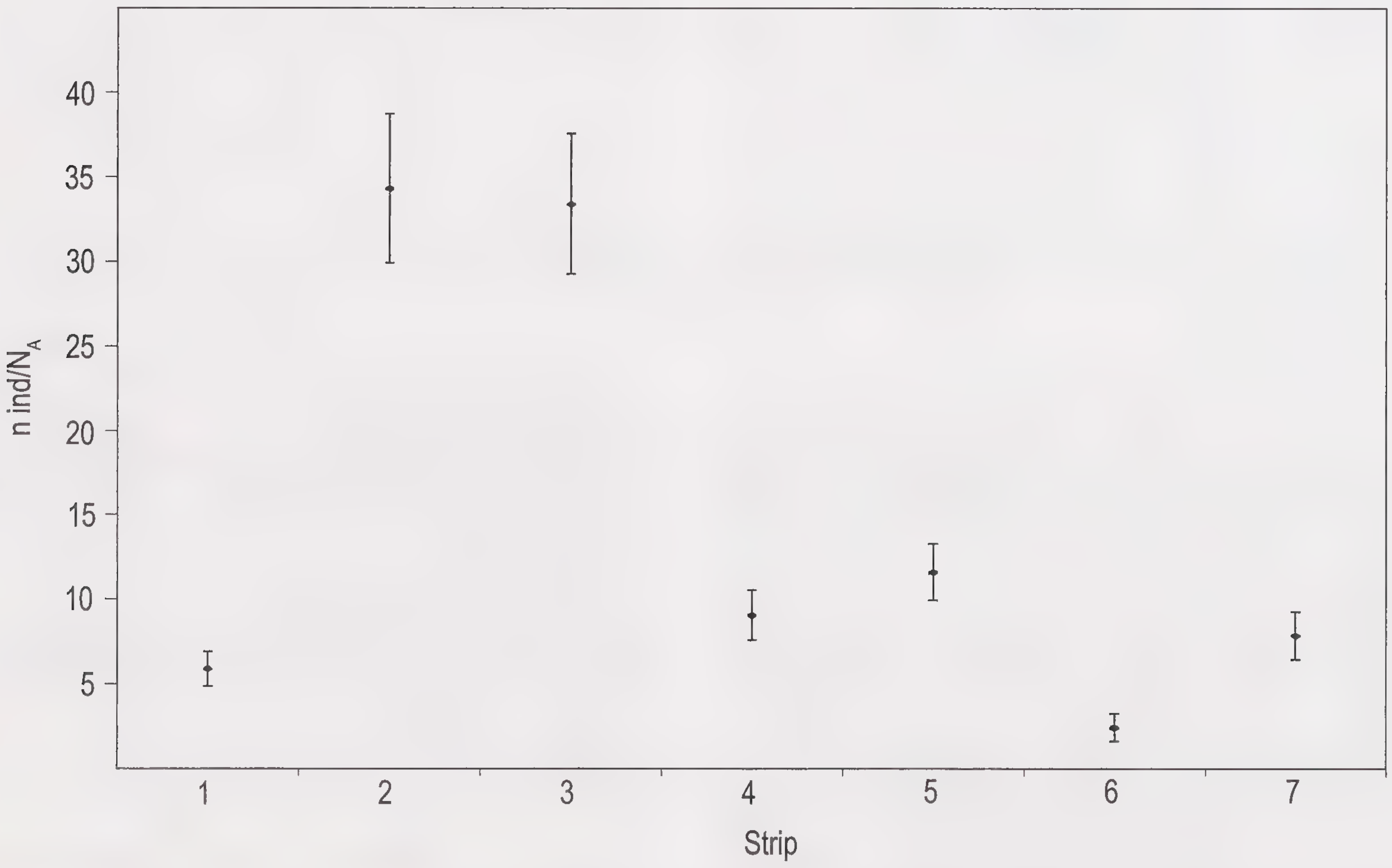

FIG. 6. Mean (± S.E.) neighbourhood size of the seven wall strips calculated over surveys. N_A: Neighbourhood Area.

DISCUSSION

The population densities recorded for *M. serpentina* were low, similar to those documented for two species of *Mastus* (Parmakelis & Mylonas, 2004), but one twentieth to one third those of other snails (Livshits, 1983; B. Baur & A. Baur, 1995; Pfenninger et al., 1996; Giokas & Mylonas, 2002).

Dispersal rate seems to be reduced (Greewood, 1974; Cameron & Carter, 1979) or increased (Cain & Currey, 1968; Oosterhoff, 1977) when densities are high. In the case of *M. serpentina*, no correlation between density and dispersal was found, perhaps reflecting the overall low density recorded. Significant differences in density on a scale of 10 m (i.e., between strips) were not correlated with environmental factors (T, % RH, and distribution of crevices, which was homogeneous, being spaces between bricks), but could possibly be correlated with spatial variation, which we did not quantify, of lichen and algal communities observed on the wall. In fact, insolation of the wall varies during the day and this may be the factor determining lichen and algal community structure (S. Munzi, comm. pers.), in addition to a possible but still not quantified effect of grazing invertebrates, including snails. Interestingly, the lowest density was recorded in the northern area (strip 6), where a crustose lichens with a particularly developed thallus (*Physconia grisea*) completely covers the wall, while only crustose lichens live on the rest of the wall. Rock-dwelling snails may have a limited ability to crawl on vegetation. Their sticky mucus enables them to adhere to vertical rock faces but makes moving on vegetation difficult (B. Baur & A. Baur, 1995). However, no data are available on the lichen preferences of *M. serpentina*. Further studies are required to test the hypothesis of significant relationships between the distributions of lichens, algae, and snails.

Recapture frequencies were in line with those in similar land snail studies (Pfenninger et al., 1996; Parmakelis & Mylonas, 2004). The decreasing trend in recapture frequencies (Fig. 4) did not seem due only to mortality, since no corresponding decrease in densities was observed. While this is not in itself proof, because increased mortality rate may be balanced by increased reproductive rate, overall observations did not support the hypothesis of higher reproductive rate. For instance, densities of juveniles remained stable over the two years. It is also unlikely that many of the non-recaptured specimens were missed: the relatively simplified environment of the wall made it easy to detect resting and hiding specimens. Specimens not recorded during certain surveys must have climbed beyond the upper limit of the survey areas. The sharp decrease in adult density from 2006 to 2007 may, on the other hand, have a demographic meaning.

Dispersal of *M. serpentina* was similar to that yearly recorded for other rock-dwelling snails: around 2.0 m for *Albinaria corrugata* (Schilthuizen & Lombaerts, 1994), 2.6 m on limestone pavement and 0.9 m on stone walls for *Chondrina clienta* (B. Baur & A. Baur, 1995).

Marmorana serpentina showed a dispersal ranging from 0.38 m to 2.90 m but with significant differences between surveys. High values coincided with the first rains after aestivation. In line with observations of other species (Yom-Tov, 1971; Cook, 2001), *M. serpentina* showed that a new epiphragm may be built after every bout of activity and is not associated with specific seasonal periods of enforced rest. In many terrestrial gastropods, breaking dormancy may not coincide with the beginning of activity after rest: individuals may become active after any minimum dormant period when conditions are favourable and may rest again immediately (Cook, 2001). It seems that hibernation and aestivation in shelled land snails have only a weak endogenous component, being largely triggered by prevailing weather conditions (Cook, 2001).

The high values of dispersal (Fig. 5) at the first rains after summer resting may be related to a demand for food and the distances travelled may increase with food deprivation (Airey, 1987; Rollo, 1991). During subsequent rainfall, snails mated, but the highest values of dispersal were lower (Fig. 5): when snails move to mate, they choose the closest partners, resulting in lower mean dispersal and the formation of groups contending for partners.

No significant direction of dispersal was detected, on spatial or temporal scales; evidence of random dispersal has been recorded for other land-snail species (A. Baur & B. Baur, 1993; Pfenninger et al., 1996; Parmakelis & Mylonas, 2004). Further, in *M. serpentina* and many other species, no evidence of homing (i.e. return to the same site by an individual) has been found, although clear fidelity to an area on a scale of 10 m x 5 m (i.e. one of the strips) was found. In two years of survey, more than half the marked specimens remained faithful to the area (circle of 1 to 3 m radius) in which they were marked (only seven specimens crossed the physical border separating wall strips). The absence of homing and directionality of dispersal, which could reasonably but mistakenly be postulated in an aggregated population structure, can be interpreted as selective responses to land life (Cook, 2001). In fact, random movements with low dispersal keep individuals faithful to an area of approximately 10 m x 5 m (i.e. one of the strips): individuals may search for resting sites, chosen simply by stopping at the first one encountered, which was previously occupied by a conspecific. Thus, homing may simply be viewed as returning to sites previously occupied by conspecifics (Cook, 2001), and in the case of the study population this is done by maintaining fidelity to a small area.

Neighbourhood size estimates for different land snails range from: 15 to 6,000 individuals (Greenwood, 1976; Crook, 1980; Cowie, 1984; Murray & Clarke, 1984; B. Baur, 1993; Schilthuizen & Lombaerts, 1994; Pfenninger et al., 1996; Parmakelis & Mylonas, 2004).

Neighbourhood size for *M. serpentina* was at the low end of this range. The study population showed significant differences in neighbourhood size at a very local scale (a 10 m scale between wall strips). Some studies (Schilthuizen & Lombaerts, 1994; Pfenninger et al., 1996; Parmakelis & Mylonas, 2004) have used an integrated approach to calculate gene flow in land snails by direct (mark-recapture experiment) and indirect (genetic variation) methods. No data on gene flow estimated by indirect methods is available for *M. serpentina*, but the patterns of population dynamics observed were similar to those of other species (low density, low dispersal and small neighbourhood size). The processes involved may be similar. Some studies indicate that when gene flow between demes is extremely limited, it can act as a homogenizing force only on a scale of a few tens of meters (Schilthuizen & Lombaerts, 1994). Beyond this scale, genetic drift and selection can play a key role in the genetic differentiation of demes (Schilthuizen & Lombaerts, 1994). Moreover, neighbourhood population structure, built by random dispersal processes in a limited spatial range, are probably a major force in generating and maintaining morphological and genetic variability (Pfenninger et al., 1996).

The present results show that population structure in *Marmorana serpentina* may be largely affected by limited and aggregated distribution due to their low dispersal capacity and fidelity to a small area. Although this conclusion stems from results gained on a non-native population, several widespread field observations on naturally occurring populations (Fiorentino et al., 2008a, b) indicate that densities can be locally lower and more aggregated than densities reported here, as well as similar to them.

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